

Highly Derived Coelomic and Water-Vascular Morphogenesis in a Starfish with Pelagic Direct Development

DANIEL A. JANIES AND LARRY R. McEDWARD

University of Florida, Department of Zoology, Gainesville, Florida 32611

Abstract. The coelomic development of the starfish *Pteraster tessellatus* (order Velatida, family Pterasteridae) is fundamentally different from that reported for all other asteroids. Coeloms arise from seven separate enterocoels that evaginate from different regions of the archenteron. The water-vascular coelomic system develops from the first five enterocoels (homologous to hydrocoel lobes) which extend radially, in a transverse orientation, from the central region of the archenteron. All other coelomic compartments derive from two enterocoels that evaginate later in development from posterior regions of the archenteron. This mode of coelom formation in *P. tessellatus* leads directly to the adult organization. We hypothesize that this altered pattern of coelomogenesis evolved from the pattern that occurs in the larvae of other spinulosacean asteroids, by a rotation in the site of origin of the anterior enterocoels relative to the archenteron. The altered pattern of coelomogenesis accounts for most of the unusual features of development in *P. tessellatus*: parallel embryonic and adult axes of symmetry, transverse orientation of the juvenile disk, absence of bilateral symmetry, absence of purely larval structures, and the lack of a metamorphosis. We conclude, contrary to previous interpretations, that *P. tessellatus* does not have a larval stage and thus represents the only described case of truly direct development in the asteroids.

Introduction

The development of *Pteraster tessellatus* is morphologically different from that of all other starfish (McEdward, 1992). *P. tessellatus* has pelagic development but does not pass through the typical asteroid larval forms, the bipin-

naia or the brachiolaria. Important features that distinguish *P. tessellatus* from other asteroids include: absence of specialized larval attachment structures (brachiolar arms and adhesive disc); accelerated development of the water-vascular system and the use of podia for attachment to the substratum at settlement; radial rather than bilateral symmetry; parallel rather than orthogonal embryonic and adult axes of symmetry; a transverse orientation of the juvenile disc; and complex morphogenesis of a supradorsal membrane.

McEdward (1992) concluded that this set of unusual developmental features in *P. tessellatus* characterized a novel type of pelagic larva in the Asterozoa. Subsequent observations led to an intriguing, but more radical, alternative interpretation: *P. tessellatus* completely lacks a larval stage and undergoes direct development (see text box: Definitions). Direct development, in which the embryo develops progressively into the juvenile, with no intervening larval features, has not been reported previously in the asteroids. Documentation of direct development would greatly expand the range of developmental diversity among starfish and would have important implications for the study of the evolution of echinoderm life cycles (McEdward and Janies, 1993).

Evaluation of the hypothesis of direct development requires additional information about the morphology of the developmental stages. Is the asteroid larval body plan present during development in *P. tessellatus*? Specifically, do internal structures develop in a bilaterally symmetrical arrangement, as is typical of starfish larvae, or is the body radially symmetrical, as is suggested by external morphology? Are there independent morphogenetic axes for early (larval) development and later (juvenile) development? Do the coeloms arise and develop in the pattern that is typical among asteroid larvae? Are there any purely

larval (transitory) structures in the development of *P. tessellatus*?

Definitions (after McEdward and Janies, 1993)

Embryo—the stages of development between fertilization and the completion of gastrulation.

Larva—the intermediate stages in development, produced by post-gastrulation morphogenesis, and eliminated by metamorphosis to the juvenile; these intermediate stages must possess transitory structures that are not involved in, and are not necessary for, morphogenesis of the juvenile.

Mesogen—the intermediate stages, transitional between the embryo and the juvenile, in the direct type of development; characterized by a complete absence of larval structures.

Juvenile—the developmental stages subsequent to the attainment of the definitive (adult) body plan, but prior to reproductive maturity.

Metamorphosis—the morphological transition from the larval body plan to the adult body plan.

Indirect development—development that involves a larval stage and a metamorphosis.

Direct development—development that lacks a larval stage and a metamorphosis; the juvenile develops progressively (directly) from the embryo, through a series of intermediate stages that are transitional towards the juvenile and do not involve the morphogenesis of any larval structures.

Developmental pattern—a set of characters (*e.g.*, development type, habitat, nutrition), each with discrete, mutually exclusive states (*e.g.*, indirect or direct; pelagic or benthic; feeding or nonfeeding) that describes features of the life cycle.

This paper describes some aspects of internal development in *P. tessellatus*, with emphasis on coelom formation and morphogenesis of the water-vascular system. Comparison with the typical pattern of indirect development via pelagic, feeding bipinnarian and brachiolarian larvae, as well as with development via modified pelagic, nonfeeding (lecithotrophic) brachiolarian larvae, reveals the coelomic and water-vascular development in *P. tessellatus* to be completely novel among asteroids. These findings, together with unusual external features of development (McEdward, 1992), lead us to conclude that *P. tessellatus* does not develop through a bilateral larval stage, nor does it undergo a metamorphosis. *P. tessellatus* represents the only known case of truly direct development in the asteroids.

Materials and Methods

Adults of the starfish *Pteraster tessellatus* Ives, 1888 (Order Velatida, Family Pterasteridae) were collected using SCUBA, from subtidal populations (5 to 20 m) at several sites near the Bamfield Marine Station (48°49'N, 125°08'W) in Barkley Sound, Vancouver Island, British Columbia, Canada, and from depths of 15 to 30 m near the Friday Harbor Laboratories (48°32'N, 123°0'W) in the San Juan Archipelago, Washington. Adults of *P. tes-*

sellatus were induced to spawn by intracoelomic injection of 2 to 5 ml (10^{-4} M) of the hormone 1-methyl adenine. Eggs (about 1000–1400 μ m in diameter) were released within 1 to 3 h after injection. The eggs developed without artificial insemination and were cultured as described by McEdward (1992).

Microscopy and 3-D reconstruction

Specimens were fixed for scanning electron microscopy (SEM) in cold osmium tetroxide (2% for 1 h) in 0.45 μ m filtered seawater, rinsed twice in distilled water, dehydrated through a graded ethanol series (30%, 50%, 70%, 15 min each), and stored in 70% ethanol. In preparation for drying, specimens were dehydrated stepwise to absolute ethanol (90%, 100%, 15 min. each), then infiltrated with hexamethyldisilazane (HMDS, Sigma Chemical Co.) for several hours. Specimens were air-dried at room temperature (Nation, 1983) in a dust-free chamber, sputter-coated with gold-palladium, and stored under desiccation.

Specimens were fixed for serial histological sectioning in Bouin's fluid (24 h), dehydrated through a graded ethanol series for 15 min in each concentration (30%, 50%, 70%), and stored in 70% ethanol. Later, specimens were dehydrated to absolute ethanol (90%, 100% 15 min each, 100% overnight), transferred to absolute ethanol with eosin y for 30 min, transferred to xylene for 30 min, infiltrated with a graded series of paraplast-xylene mixtures (at 56°C under vacuum), then embedded in paraplast. Embedded specimens were serially sectioned at 7 or 12 μ m, and stained in hematoxylin-eosin. Some specimens were partially sectioned. The tissue remaining in the block was prepared for SEM by dissolving the paraplast in xylene and drying the tissue with HMDS, as described above.

Serial sections (about 80 per mesogen) were examined and photographed with a compound light microscope. Three-dimensional reconstruction was achieved as follows. Sequential sections were aligned visually for tracing. The outer edges of the body wall, coelomic compartments, and developing gut were traced as color-coded contours onto paper with the aid of a camera lucida drawing tube. The tracings were marked with a set of fiduciary points for alignment during digitization. The x, y, and z coordinates of points along the contours were entered in a computer with a digitizing tablet and stored as ASCII files. These coordinate data were then plotted as a graphic image of each section and stored as a bitmapped file of raw eight-bit color pixel data. Digitization and data conversion were done with programs written for this purpose (commented Pascal source code for DOS systems can be obtained from McEdward). Entire series of sections (bitmapped files) were imported into the program NIH Image 1.44 (a public domain program for Apple Macintosh computers available over Internet by anonymous ftp from zippy.nimh.

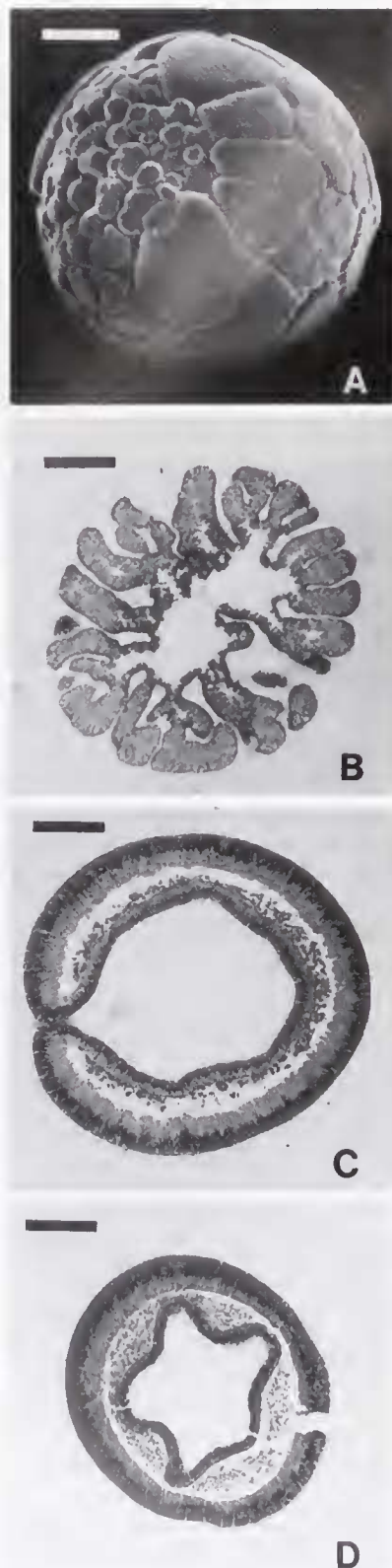


Figure 1. Early development of the *Pteraster tessellatus* embryo. A. SEM of early (1d) blastula showing irregular pattern of cleavages and blastomeres of various sizes. B. Histological section of 1d 12h wrinkled blastula showing deep folds in blastular wall and blastocoel. C. Longi-

nih.gov [128.231.98.32]). The regions bounded by endodermal and mesodermal contours in each section were filled with color to allow production of solid (rather than "wire-frame") reconstructions. These filled images were saved as a series of files in TIFF format. Stacking and projecting routines (based on a brightest point algorithm) in NIH Image were used to create 3-D reconstructions. Selected layers, such as the ectoderm could be removed by adjustment of the transparency bounds allowing visualization of internal structures.

Results

Overview of development in Pteraster tessellatus

External features of development were described by McEdward (1992). Here we summarize that description and add some additional observations. The pattern of early cleavages was irregular and resulted in blastomeres of various sizes without a regular arrangement (Fig. 1A). As cleavage progressed the blastomeres became smaller, and the surface of the embryo acquired a smooth appearance. The wall of the blastula was thrown into deep folds resulting in a wrinkled blastula stage (Fig. 1B). McEdward (1992) had reported that, during gastrulation, initiation of archenteron formation in *P. tessellatus* was correlated with the loss of folding of the blastular wall in the vegetal hemisphere of the embryo. Our study confirmed that subsequent enlargement of the archenteron was accompanied by a progressive loss of folding of the blastular wall, from the equatorial region to the animal pole of the embryo. These observations suggest that the formation of the archenteron may be due primarily to involution and not ingression. The gastrula elongated along the animal-vegetal axis and acquired an ovoid body form, just before hatching at 3 days. Within 1 to 2 days of hatching, an ectodermal depression produced a groove completely around the circumference that divided the body into anterior and posterior regions (Fig. 3A).

The oral surface of the juvenile corresponded to the anterior region of the mesogen (= animal pole of the embryo), and the aboral surface of the juvenile corresponded to the posterior end of the mesogen (= embryonic vegetal pole and blastopore) (Fig. 2). Consequently, the juvenile disc developed in a transverse orientation with respect to the anterior-posterior and animal-vegetal axes. All of the stages of development were characterized by radial, rather than bilateral, symmetry. Morphogenesis of the supra-

tudinal section of 2d 5h gastrula showing the large archenteron and small blastocoelic space. The posterior end, as indicated by the blastopore is oriented to the left. D. Transverse section, perpendicular to the anterior posterior axis of a 4d 16h elongate mesogen, showing five lateral pouches evaginating simultaneously from the equatorial region of the archenteron.

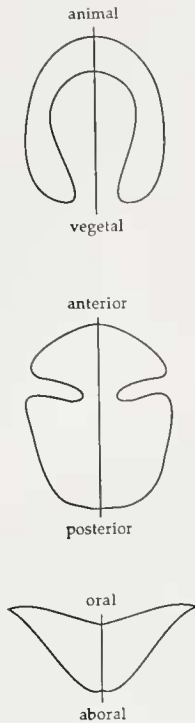


Figure 2. Diagram illustrating the orientation of the axes of symmetry of developmental stages of *Pteraster tessellatus*. Top, animal-vegetal axis of the embryonic stages, zygote to gastrula; middle, anterior-posterior axis of the mesogen; bottom, oral-aboral axis of the juvenile and adult starfish.

dorsal membrane began at 5 to 8 days with the formation of five broad marginal bulges around the circumference of the body, immediately posterior to the groove (Fig. 3A, 4A). The marginal bulges became bilobed at 8 to 10 days (Fig. 4A, O) and eventually divided to produce a total of 10 distinct marginal lobes at 16 days. Five additional lobes developed at the aboral pole of the body at 11 to 13 days. All 15 lobes fused at 17 to 19 days, resulting in a complete supradorsal membrane above the aboral body wall (McEdward, 1992, pp. 181–183). In the adult, the supradorsal membrane encloses a space, the nidamental chamber, that protects, ventilates, and perhaps nourishes young in pterasterids that brood (McClary and Mladenov, 1990). Functional podia, arranged in five clusters, emerged from the circumferential groove at 9 days, long before the development of juvenile arms (at 2.5 months). Early development of the podia is important because the mesogen of *P. tessellatus* lacks the brachiolar arms and adhesive disk of other pelagic nonfeeding larvae (Fig. 3A, 4A). Podia of *P. tessellatus* are used for attachment to the substratum at settlement at 10 to 12 days. Each podial cluster initially consisted of a pair of podia and a terminal podium. Three to four additional pairs of podia were added by 28 days. The juvenile mouth did not form until the second month, and distinct arms were not present in most

P. tessellatus juveniles until the third month (McEdward, 1992).

Internal development of Pteraster tessellatus

Gastrulation. At 2 to 3 days of development in *P. tessellatus*, the archenteron widened within the gastrula. The interior of the ovoid stage contained a large archenteron that extended from the blastopore at the posterior (= vegetal) end all the way to the anterior (= animal) end. The archenteron nearly filled the interior of the body, causing the ectodermal and mesendodermal cell layers to lie close together and greatly reduced the blastocoelic space (Fig. 1C). The blastopore closed between days 3 and 4 resulting in a completely closed archenteron sac. The archenteron did not join with the animal ectoderm to form a stomodeal opening. *P. tessellatus* produces large, yolky mesogens that do not feed on particulate food.

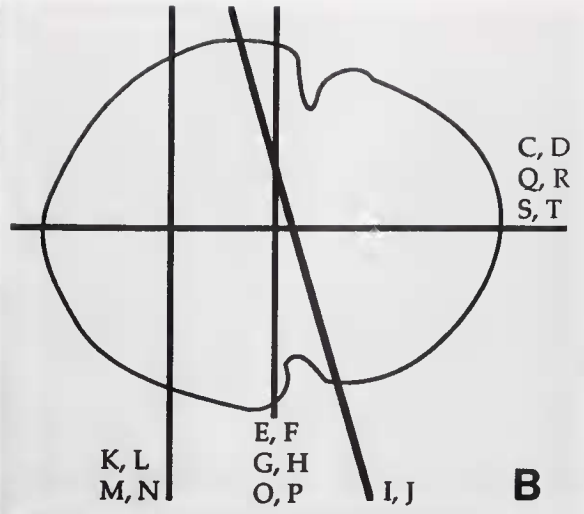
Morphogenesis of the water-vascular system. At 4 days, five lateral coelomic pouches (enterocoels) evaginated simultaneously from the equatorial region of the archenteron (Fig. 1D, 3E–H). The five enterocoels were arranged symmetrically around the circumference of the archenteron in a transverse plane (*i.e.*, perpendicular to the anterior-posterior axis of the mesogen; Fig. 2, 7III B). These five enterocoels were hydrocoelic in nature because they became the coelomic lining of the water-vascular system (*i.e.*, radial canals, podia, ampullae, and circumoral ring canal). Initially, these hydrocoel lobes were broad, simple evaginations from the archenteron (Fig. 1D). The hydrocoel lobes elongated as they extended radially towards the ectodermal body wall. The hydrocoel lobes remained connected to the archenteron throughout much of the development of the water-vascular system. The hydrocoel lobes and their relationship to the archenteron are evident in transverse section (Fig. 3E–H) and in 3-D reconstruction (Fig. 5A, B). A diagram of the typical adult asteroid water-vascular coelomic system, perihemal coelomic system, hemal system, and axial complex (Fig. 6) and a table of terminology used in this paper, cross referenced to that of Hyman (1955), (Fig. 8) are provided to aid in visualizing the morphogenesis of *P. tessellatus*.

At 5 days, the distal ends of the hydrocoel lobes began to contact the overlying ectoderm (Fig. 3E, F). At the time and location of this contact, the ectoderm began to fold inward to produce the circumferential groove. The groove formed just anterior to the hydrocoel, so that the contact with the hydrocoel lobes occurred along the posterior wall of the groove (Fig. 3C–J).

The proximal and central portions of each hydrocoel lobe developed into a radial canal. The distal part of each hydrocoel lobe widened and then bifurcated to form the coelomic lining of the first pair of podia (Fig. 3G, H). The coelomic lining of each terminal (unpaired) podium de-



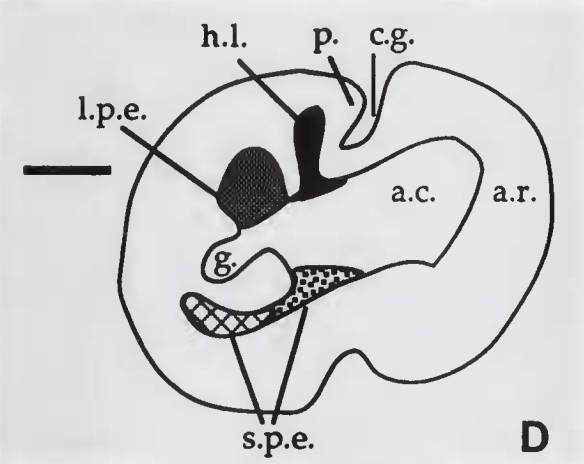
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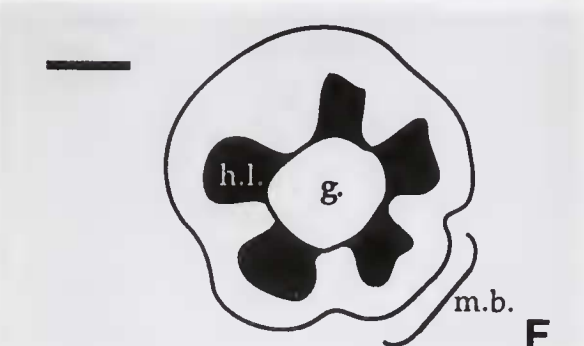
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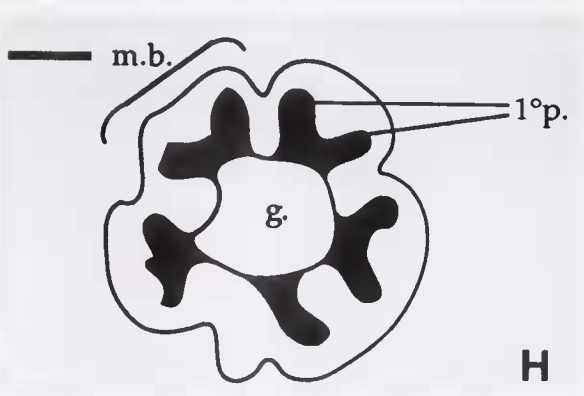
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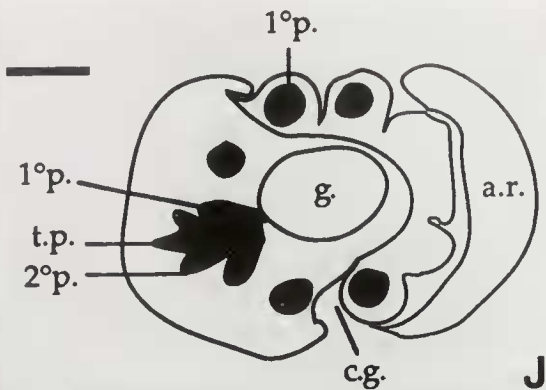
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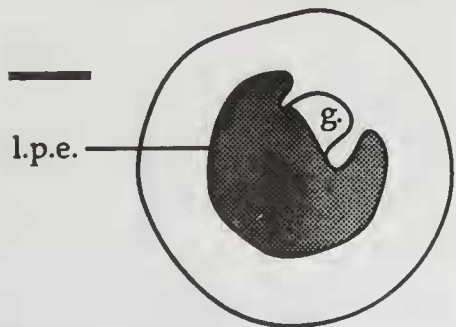
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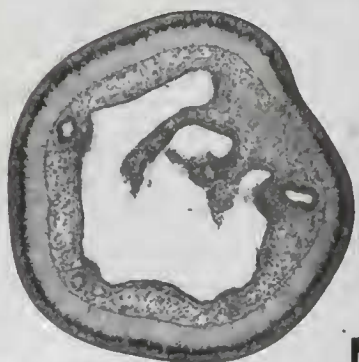
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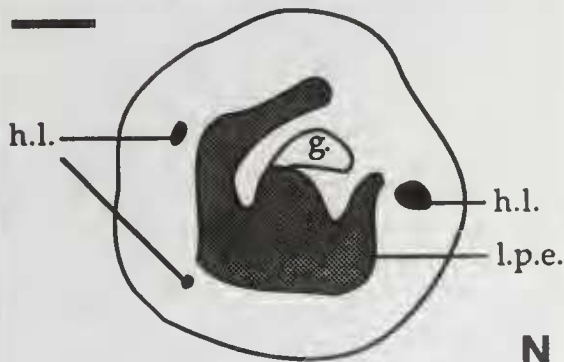
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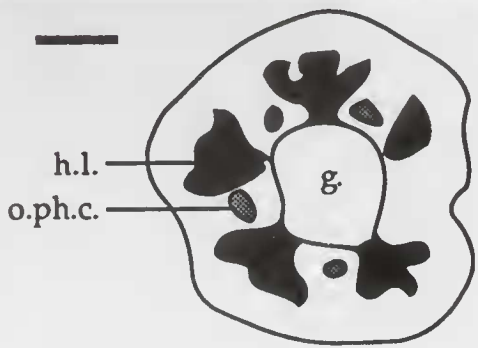
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Figure 3. (Continued)

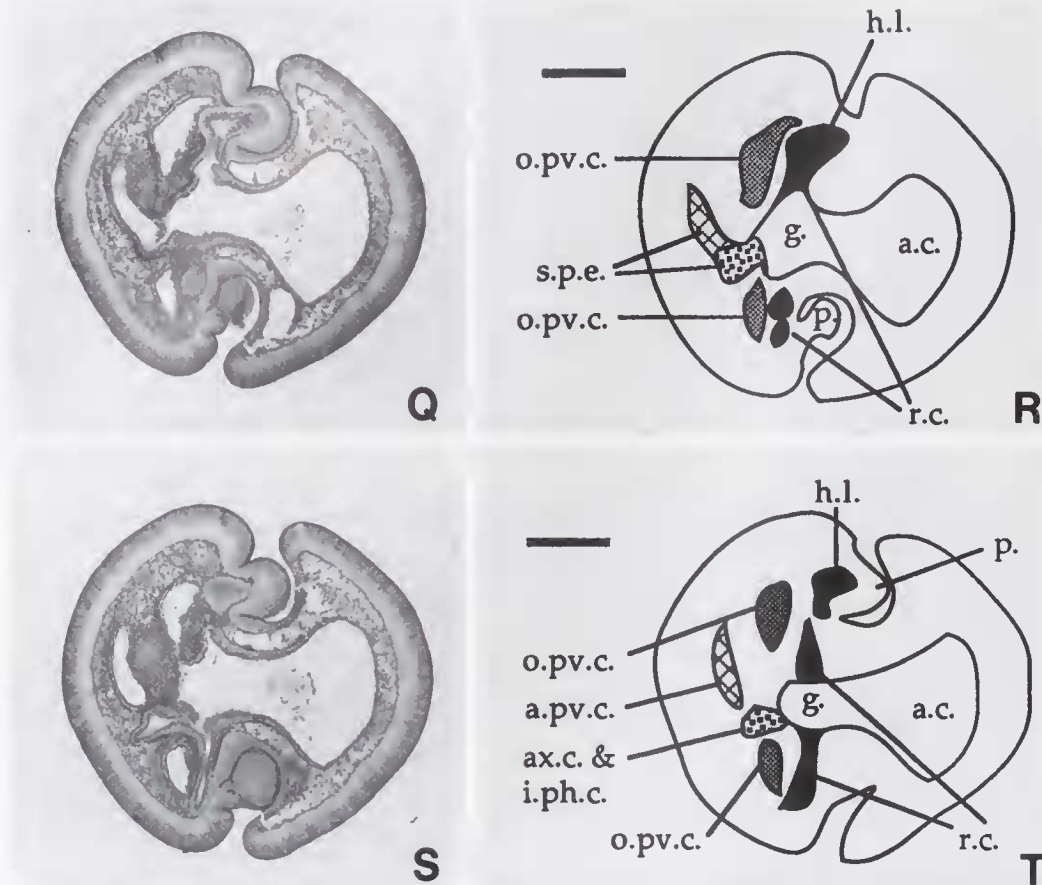


Figure 3. Internal morphogenesis of the early (about 6–8d) mesogen of *Pteraster tessellatus*. Magnification is the same in all panels and scale bar equals 0.2 mm. In all lateral views the posterior of the mesogen is oriented to the left. A. SEM, lateral view of 6d mesogen, showing circumferential groove dividing anterior and posterior body regions. Podia are visible in the circumferential groove. B. Drawing of lateral view of mesogen in panel A showing location and orientation of planes of section for the following panels of this figure. C–T. Paired light micrographs and interpretive diagrams of histological sections. See Table 1 for abbreviations. C, D. Longitudinal section of 6d mesogen showing origin of the enterocoels from the archenteron and relationship of circumferential groove to the hydrocoels. E, F. Transverse section of 5d 8h mesogen showing the first five evaginations (hydrocoels) in pentaradial symmetry around the circumference of the archenteron and their early contact with the overlying ectoderm. G, H. Transverse section of 6d mesogen showing the bifurcation of the distal part of each hydrocoel lobe that forms the coelomic lining of the first pair of podia. I, J. Oblique section of 7d mesogen showing the coelomic lining of the terminal unpaired podium forming as an extension from the cleft of the original bifurcation and the coelomic lining second pair of podia evaginating between the terminal podium and the first pair. K, L. Transverse section through a 5d 8h mesogen showing the large posterior enterocoel evaginating as a large crescent shape from the extreme posterior region of the archenteron. M, N. Transverse section of 6d mesogen showing the large posterior enterocoel encircling the gut and enveloping the posterior side of the hydrocoel lobes. O, P. Transverse section of 6d mesogen showing four of the five initial small pouches growing orally from the oral perivisceral coelom between the hydrocoel lobes to originate the outer oral perihemal ring coelom. Q, R. Longitudinal section of 6d 16h mesogen showing the enterocoels, especially the small posterior enterocoel and its mixed set of fates of the (*i.e.*, axocoelic and somatocoelic). S, T. Longitudinal section of 6d 16h mesogen (same mesogen as section in Q, R) showing the somatocoelic derivative (the aboral perivisceral coelom) separating from the distal region of the small posterior enterocoel and moving to the extreme posterior of the body. The proximal region of the small posterior enterocoel develops into the inner oral perihemal ring coelom and likely contributes to the coelomic and hemal axial complex, such as the axial coelom and madreporic vesicle.

Table 1

Abbreviations used in Figures 3 and 4

Abbreviation	Description
1°p.	coelomic lining of the primary podia of the water-vascular system
2°p.	coelomic lining of the secondary podia of the water-vascular system
a.	ampulla of the podia of the water-vascular system
a.c.	anterior compartment of the archenteron
a.p.v.c.	aboral perivisceral coelom
a.r.	anterior region of the mesogen
ax.c.	axial coelom
c.g.	circumferential groove
co.r.c.	circumoral ring canal of the water-vascular system
g.	gut
h.l.	hydrocoel lobe of the water-vascular system
hp.c.	hydropore canal
i.ph.c.	inner oral perihemal ring coelom
l.c.	lateral canal of the water-vascular system
l.p.e.	large posterior enterocoel
m.b.	marginal bulge of the mesogen
o.ph.c.	outer oral perihemal ring coelom
o.p.v.c.	oral perivisceral coelom
p.	ectodermal covering of the podia
r.c.	radial canal of the water-vascular system
s.p.e.	small posterior enterocoel
l.p.	coelomic lining of the terminal podium of the water-vascular system

veloped as an extension from the cleft of the original bifurcation. At 7 days, the coelomic lining of the second pair of podia evaginated between the terminal podium and the first pair (Fig. 3I, J). In the region of the hydrocoel lobes, the ectoderm of the circumferential groove thickened, enveloped the developing coelomic linings, and produced the epidermal covering of the podia. In subsequent development, additional pairs of podia were added immediately proximal to the terminal podium as the radial canals elongated (Fig. 4M, N).

The five hydrocoel lobes remained connected to the gut but were otherwise independent of each other during the early development of the radial canals and podia. Later, these five independent evaginations were connected by a coelomic tube (ring canal) that encircled the gut. At 8 to 9 days, each radial canal separated from the archenteron by a constriction of the oral side of its proximal end. Concurrently, the aboral portion of the proximal end of each radial canal produced small lateral evaginations in the transverse plane of the body. These evaginations grew around the circumference of the archenteron, met in the interradia, and fused to complete the circumoral ring canal (Fig. 4E–N, 5B).

The ampullae developed by an expansion of the coelomic lining on the aboral side of each podium. By 8 days, the ampullae of the first two pairs of podia had greatly

enlarged and extended up against the oral perivisceral coelom (Fig. 4C, D). At 8 to 9 days, the hydropore canal developed as a long tubular invagination from the aboral ectoderm in the extreme posterior region of the body. It extended orally and joined with the developing circumoral ring canal (Fig. 4E, F, I, J, K, L, S, T, and 5B). The hydropore canal was an ectodermal structure that was conspicuous in early development because it stained very deeply. We assumed the hydropore canal gave rise to the stone canal of the adult as is typical of asteroids although we did not trace its development beyond 12 days.

The completion of the major water-vascular components (circumoral ring canal, radial canals, podia with expanded ampullae, and hydropore canal) at 8 to 9 days corresponded to the time at which a mesogen possessed functional podia that could be extended from the body and used to adhere to the substratum. In laboratory cultures, settlement occurred as early as 1 to 2 days after the completion of a functional water-vascular system (McEdward, 1992).

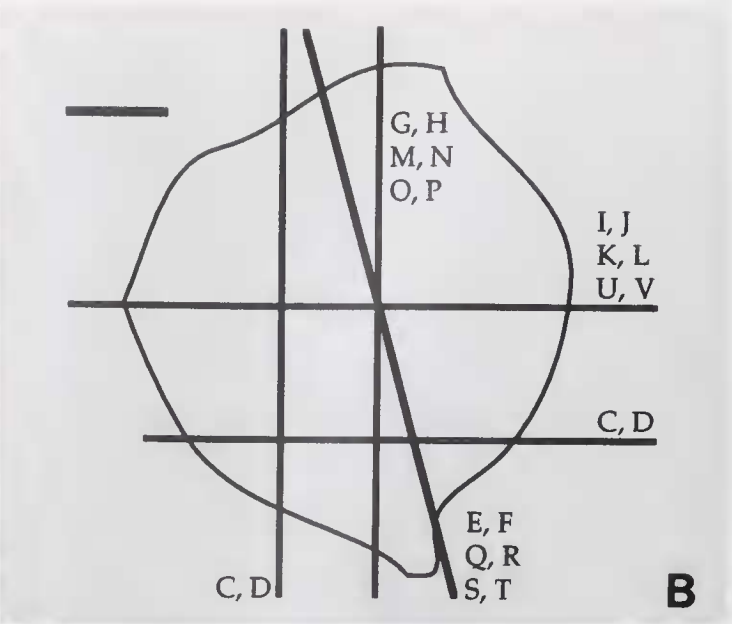
Formation of the perivisceral coeloms and axial complex. Soon after the evagination of the hydrocoel lobes from the archenteron, two additional enterocoelic evaginations appeared (Fig. 3C, D, K, L, Q–T, 5A, B): (1) a large posterior enterocoel (= 6th of 7 enterocoels) whose fate was to become the oral perivisceral coelom which in turn produced the outer oral perihemal ring coelom in the juvenile; and (2) a small posterior enterocoel (= 7th of 7 enterocoels) that formed the axial and inner oral perihemal coeloms and the aboral perivisceral coelom.

The large posterior enterocoel developed from the extreme posterior region of the archenteron at 4 to 5 days. Initially, this enterocoel had the shape of a very large crescent lying in a plane transverse to the anterior-posterior axis of the mesogen (Fig. 3K, L, 5A). By 5 days, this large posterior enterocoel assumed the adult location of the oral perivisceral coelom: it encircled the gut and enveloped the posterior side of the hydrocoel (especially the ampullae of the podia) (Fig. 4C, D; 3M, N; 5A). At 6 days, the oral perivisceral coelom developed five small pouches that grew orally (= anteriorly) between the hydrocoel lobes in interradial positions (Fig. 3O, P). These processes then grew laterally and fused in the radii to form the outer oral perihemal ring coelom (Fig. 4O, P).

At 4 to 6 days, the small posterior enterocoel evaginated from the archenteron posterior to the hydrocoel and slightly anterior to site of evagination of the large posterior enterocoel (Fig. 3C, D, M, N; 5A). The small posterior enterocoel subdivided into a complex set of coeloms. At 6 days, the aboral perivisceral coelom separated from the distal region of the small posterior enterocoel and moved to the extreme posterior of the body (Fig. 3Q–T; 5A). The proximal region of the small posterior enterocoel formed a crescentic coelom near the aboral, inner surface of the



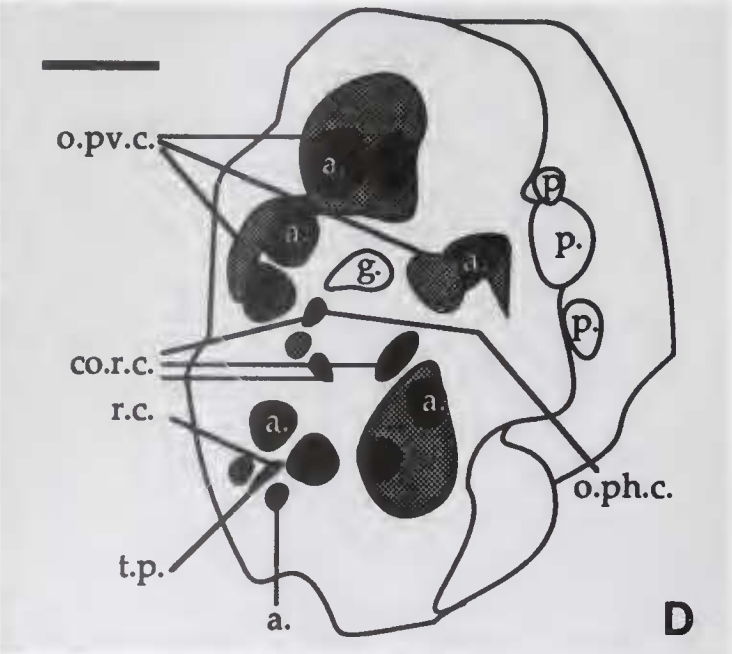
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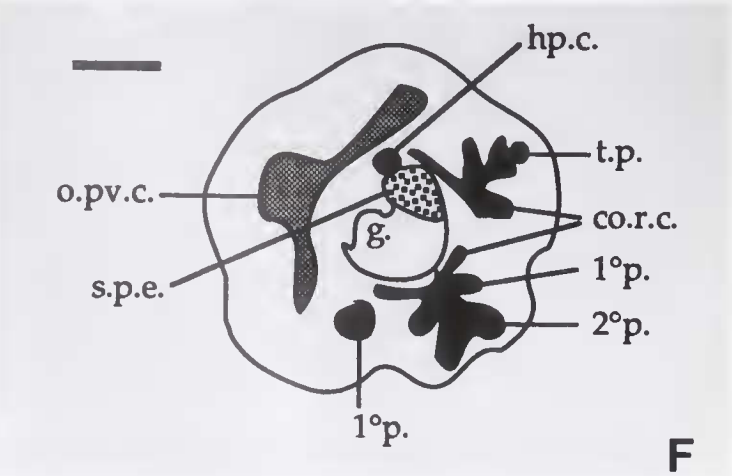
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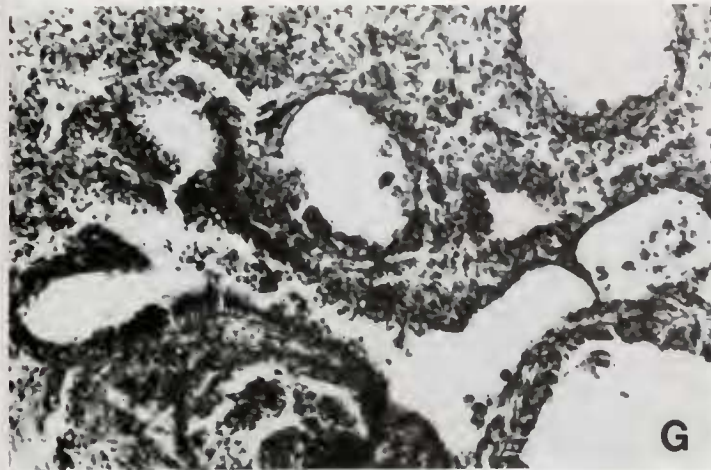


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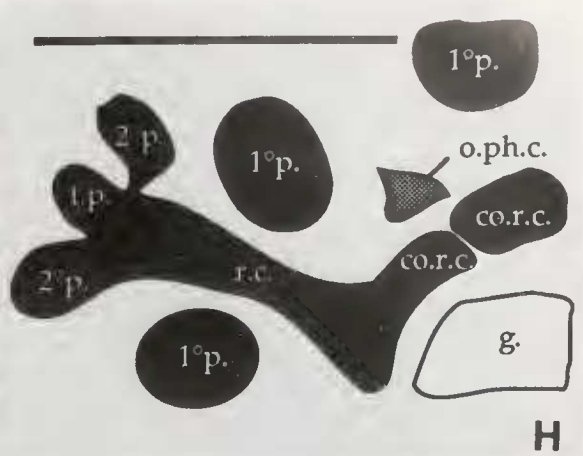


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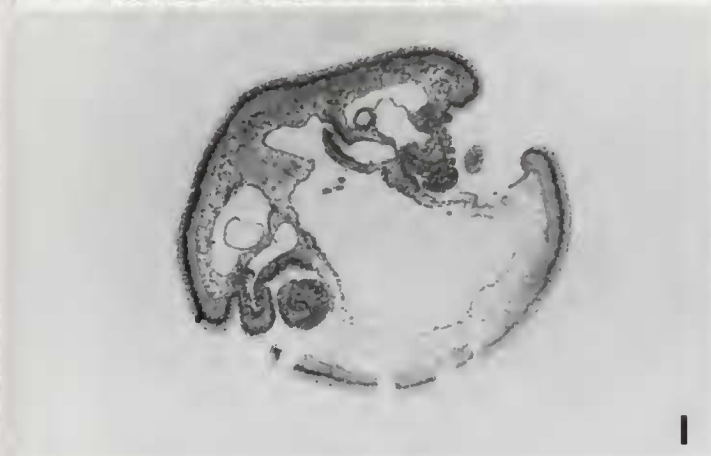
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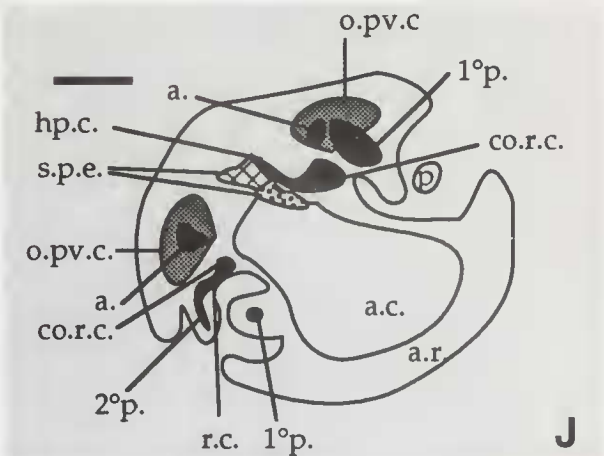
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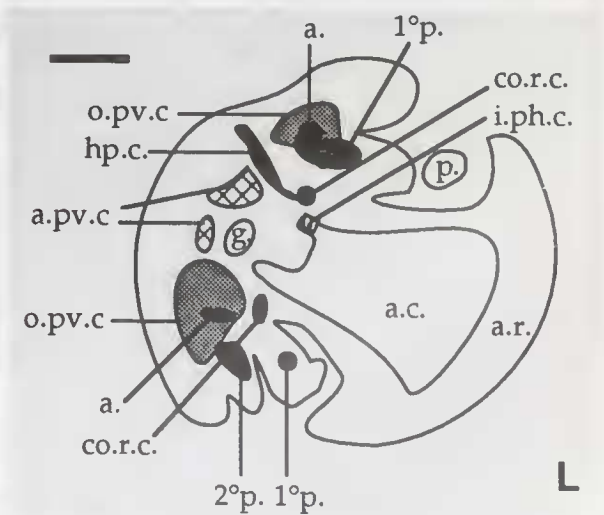
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Figure 4. (Continued)

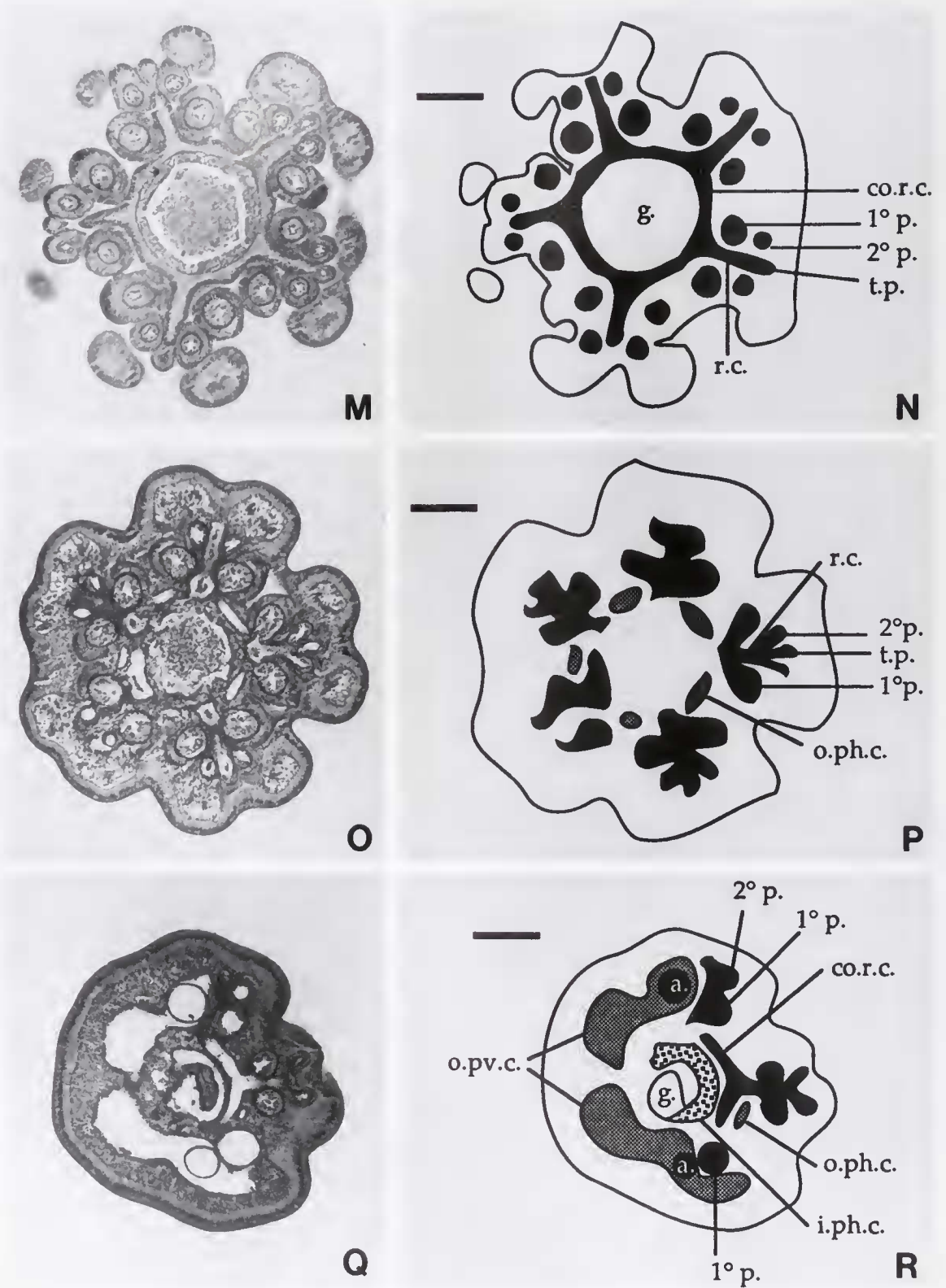


Figure 4. (Continued)

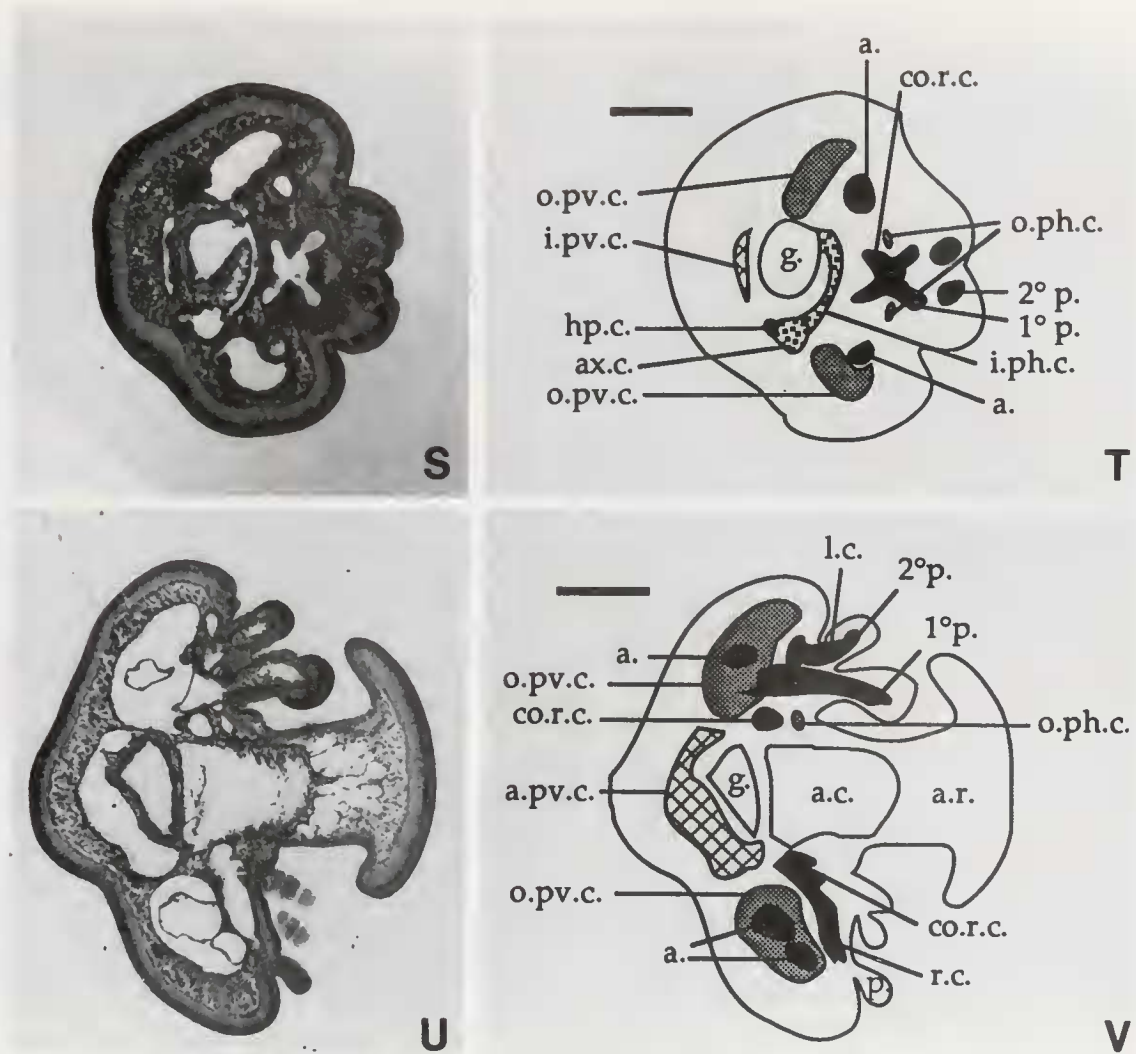


Figure 4. Morphogenesis of the late (≈ 9 –11d) mesogen of *Pteraster tessellatus*. Magnification is equal in all panels (except G, H) and all scale bars equal 0.2 mm. In all lateral views the posterior of the mesogen is oriented to the left. See Table I for abbreviations. A, SEM, lateral view of 9d mesogen showing five marginal bulges and well developed podia. B, Drawing of lateral view of mesogen in panel A showing location and orientation of planes of section for the following panels of this figure. C, D, SEM and interpretive diagram of 9d mesogen sectioned in two planes and oriented obliquely to the viewer. Transverse face revealing the oral perivisceral coelom and elements of the hemal and water-vascular system in the oral region of the mesogen, especially the ampullae of the podia. Longitudinal face revealing an ampulla and the ectodermal covering of a cluster of podia. E–V, Paired light micrographs and interpretive diagrams of histological sections. E, F, Slightly oblique section of 9d mesogen showing the proximal lateral evaginations of the radial canals that fuse to form the circumoral ring canal of the water-vascular system. Also, the proximity of the hydropore canal to the small posterior enterocoel is visible. G, H, Transverse section at high magnification of an 8d ambulacrum revealing the proximal lateral evaginations of the radial canals that form the circumoral ring canal and showing the early development of a portion of the outer oral perihemal ring coelom. I, J, K, L, Two longitudinal sections from the same 10d mesogen. These illustrate the ectodermal origin of the hydropore canal, its confluence with the middle region of the small posterior enterocoel to form part of the axial complex, and the connection of the hydropore canal to the circumoral ring canal. M, N, Transverse section through the completed water-vascular system of an 11d mesogen. O, P, Transverse section through the same 11d mesogen as in panels M, N. This section is slightly aboral to M, N and hence reveals the outpockets of the oral perivisceral coelom that form the outer oral perihemal ring coelom. Q, R, Oblique section through 9d mesogen showing formation of the crescentic shaped inner oral perihemal ring coelom from the proximal region of the small posterior enterocoel. This view illustrates the proximity of the inner oral perihemal ring coelom with the circumoral ring canal of the water-vascular system. S, T, Oblique section of 7d 16h mesogen showing the formation of the axial complex from the confluence between the inner oral perihemal ring coelom and the hydropore canal. U, V, Longitudinal section of 11d mesogen showing an adult internal organization. At this stage the anterior compartment is in the process of transferring the contents of the anterior region of the mesogen to the gut in order to fuel development.

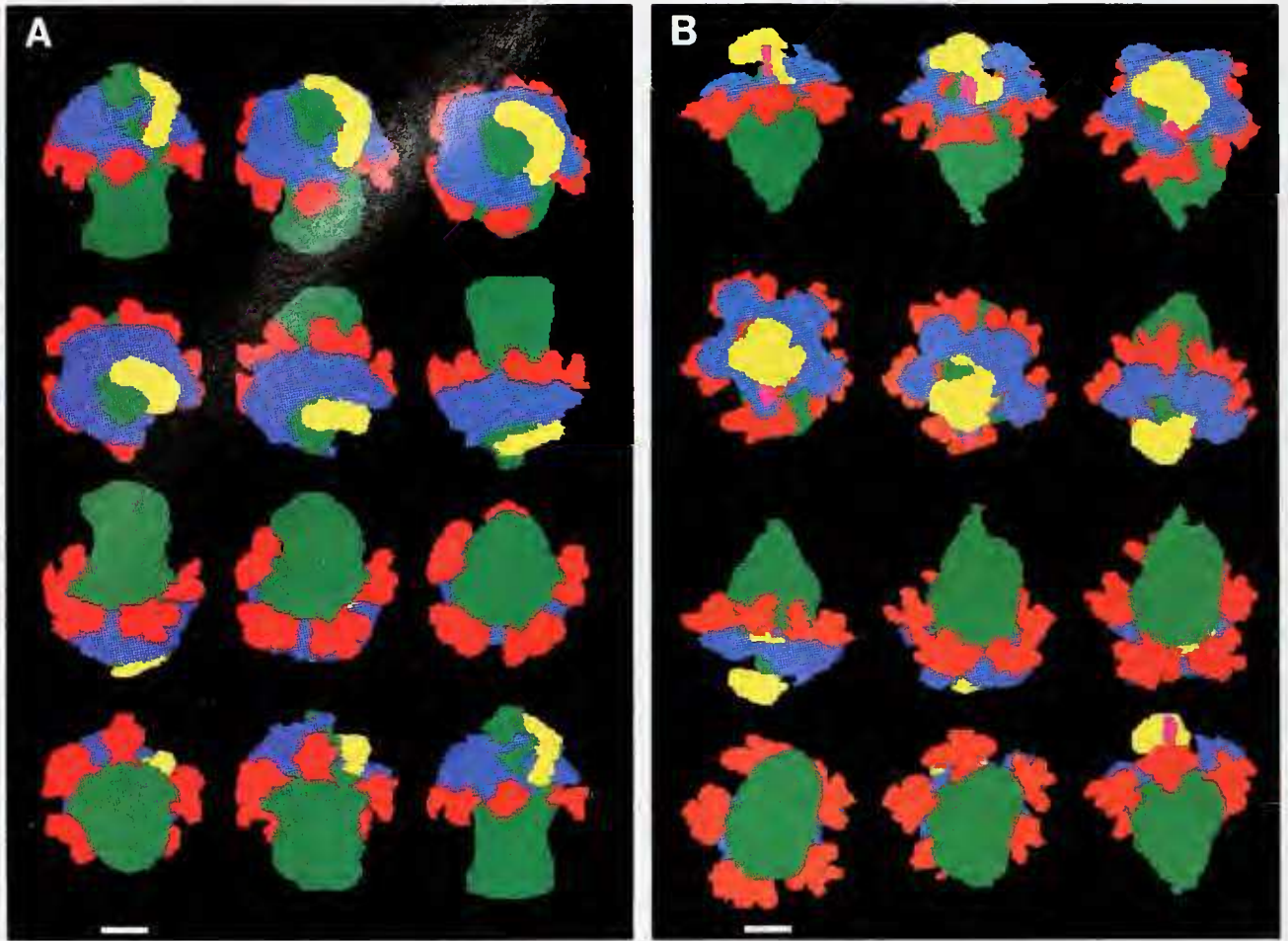


Figure 5. Two 3-D reconstructions of internal features (mesoderm and endoderm) of two stages (a, 6d, b, 9d) of a *Pteraster tessellatus* mesogen. Each half page panel contains a montage of 12 views of a single specimen as a series of 30° rotations through a total of 360°. The rotational sequence begins in the upper left and progresses across the top row to the right. Subsequent rows are also read left to right. The initial (upper left) and final (lower right) views are oriented with the posterior of the mesogen up. The identity of each structure is color keyed as follows: red = water-vascular coelomic lining, green = gut and anterior compartment, yellow = small posterior enterocoel, blue = large posterior enterocoel, and purple = hydropore. Scale bar = 0.2 mm.

circumoral ring canal of the water-vascular system (Fig. 4Q, R). This crescentic coelom developed into the inner oral perihemal ring coelom. The middle region of the small posterior enterocoel was confluent with the hydropore canal (Fig. 3Q–T; 4E, F, I–L, S, T). The region of contact between these coeloms likely formed some substructures of the coelomic and hemal axial complex, such as the axial coelom and madreporic vesicle. However, a comprehensive and definitive description of the development of the axial complex will require substantial additional study.

Development of the gut and anterior compartment. A great deal of coelomic morphogenesis occurred in *P. tessellatus* while the seven enterocoels remained confluent via the central portion of the archenteron. Masterman

(1902) described a similar arrangement of connected enterocoels and archenteron as a “mesenteron” in *Henricia sanguinolenta* (formerly *Cribella oculata*). This term is useful in describing the internal development of *P. tessellatus*. At 4 to 5 days, in *P. tessellatus*, despite the confluence among all seven of the enterocoels, the gut (endoderm) was histologically differentiated from the coelomic (mesodermal) regions of the mesenteron. The gut was delineated as a deeply staining, thickened epithelial region located posterior to the five hydrocoel lobes and in between the two posterior enterocoels (Fig. 3C, D, Q–T; 5A, B).

The region of the mesogen anterior to the circumferential groove was filled peripherally with yolk and fibrous material, but also contained an epithelial layer that en-

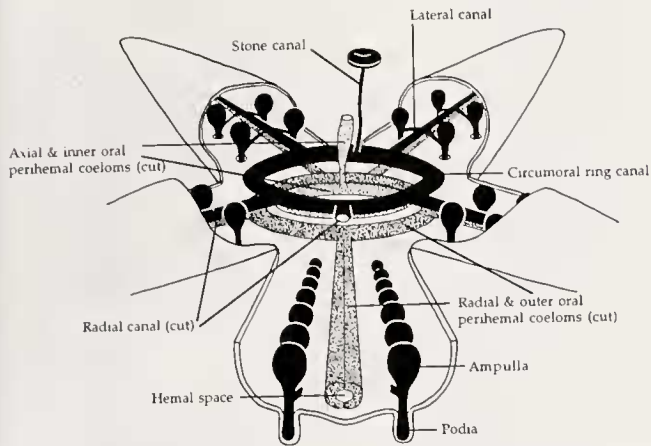


Figure 6. Drawing of the internal anatomy of a typical adult asteroid showing the arrangement of water-vascular and perihemal coelomic systems as well as components of the hemal system. See Figure 8 for an interpretation of the stippling.

closed a large, central internal compartment (Fig. 3C, D, Q–T; 4I–L). The epithelial compartment was not the product of enterocoely but was simply the anterior of the archenteron produced by gastrulation. Hence we do not believe it is properly termed a coelom but rather an anterior compartment of the gut. The anterior compartment remained confluent with the gut region of the archenteron throughout juvenile development. Identifiable structures did not develop in the anterior region of the mesogen and its blastocoelic contents were depleted during development (Fig. 4U, V).

Discussion

P. tessellatus is radially symmetrical throughout development, lacks all larval structures, and does not undergo a metamorphosis. In addition, the coeloms arise from seven separate enterocoels that evaginate from different regions of the archenteron. The water-vascular coelomic system develops from the first five enterocoels (homologous to hydrocoel lobes) that extend radially, in a transverse orientation, from the central region of the archenteron. All other coelomic compartments develop from two enterocoels that evaginate later in development from posterior regions of the archenteron. This mode of coelom formation in *P. tessellatus* leads directly to the adult organization. From these results, we conclude that *P. tessellatus* represents the first case of truly direct development described in the asteroids.

Did direct development evolve through modification of the typical pattern of asteroid larval development? The considerable morphological and ecological diversity of asteroid larvae seems to argue against the idea of a typical larva or typical pattern of development. However, only a

single component of development, coelomogenesis, underlies all of the important features characterizing direct development in *P. tessellatus*: radial symmetry, transverse disc, parallel embryonic and adult axes, and lack of larval organization. If there is a general pattern of coelom development among asteroids, or if the starfish most closely related to *P. tessellatus* share common features of coelomogenesis, then there would be a basis from which to explore the morphogenetic changes that could lead to the evolution of direct development. In the following sections, we analyze the literature on asteroid larvae and conclude that there are extremely conservative features of coelomic development. Then we present a hypothesis to explain the evolution of the highly modified coelomogenesis that we have described in *P. tessellatus*.

Patterns of asteroid coelomogenesis

Asteroids with indirect development and pelagic feeding larvae. Development from small eggs (about 100–200 μm in diameter) via feeding bipinnarian and feeding brachiolarian larvae is the ancestral pattern in asteroids (Strathmann, 1974, 1978; McEdward and Janies, 1993). In species with feeding bipinnarian larvae, the coeloms develop from a pair of enterocoels that evaginate from the tip of the archenteron (Fig. 71A–B) (e.g., *Asterias rubens*, Gemmill, 1914; see also reviews by Hörstadius, 1939; Hyman, 1955; Chia and Walker, 1991). The enterocoels develop into three pairs of coeloms (from anterior to posterior: axocoels, hydrocoels, and somatocoels) (Fig. 71C). The somatocoels pinch off from the enterocoels as separate coeloms early in larval development, but the axocoels and hydrocoels are often confluent via small coelomic tubes and hence are considered axohydrocoels by some (Hyman, 1955). However, each coelomic sac or region can be considered to have a separate role in organogenesis (Fig. 7, 8). By the brachiolarian stage, the left and right axocoels fuse in the anterior region of the larva to form a single coelom (axocoel) in the shape and orientation of an inverted U (Fig. 71D) (Gemmill, 1914). The axocoel extends anteriorly into the preoral lobe, which is defined by its location anterior to the larval mouth. This portion of the axocoel is termed the preoral coelom (or anterior coelom). The preoral coelom extends into the lumen of the brachiolar arms (Barker, 1978), if present.

Paxillosids with indirect development and pelagic feeding larvae. Asteroids in the order Paxillosida with pelagic feeding development have only a bipinnarian stage. These are termed, “non-brachiolarian larvae” because they lack brachiolar arms and the associated coelomic projections (Oguro *et al.*, 1976). Despite this, these larvae undergo the typical pattern of coelomogenesis (described above and in Fig. 71A–D) and have a well-developed preoral coelom that extends anteriorly into the preoral lobe of

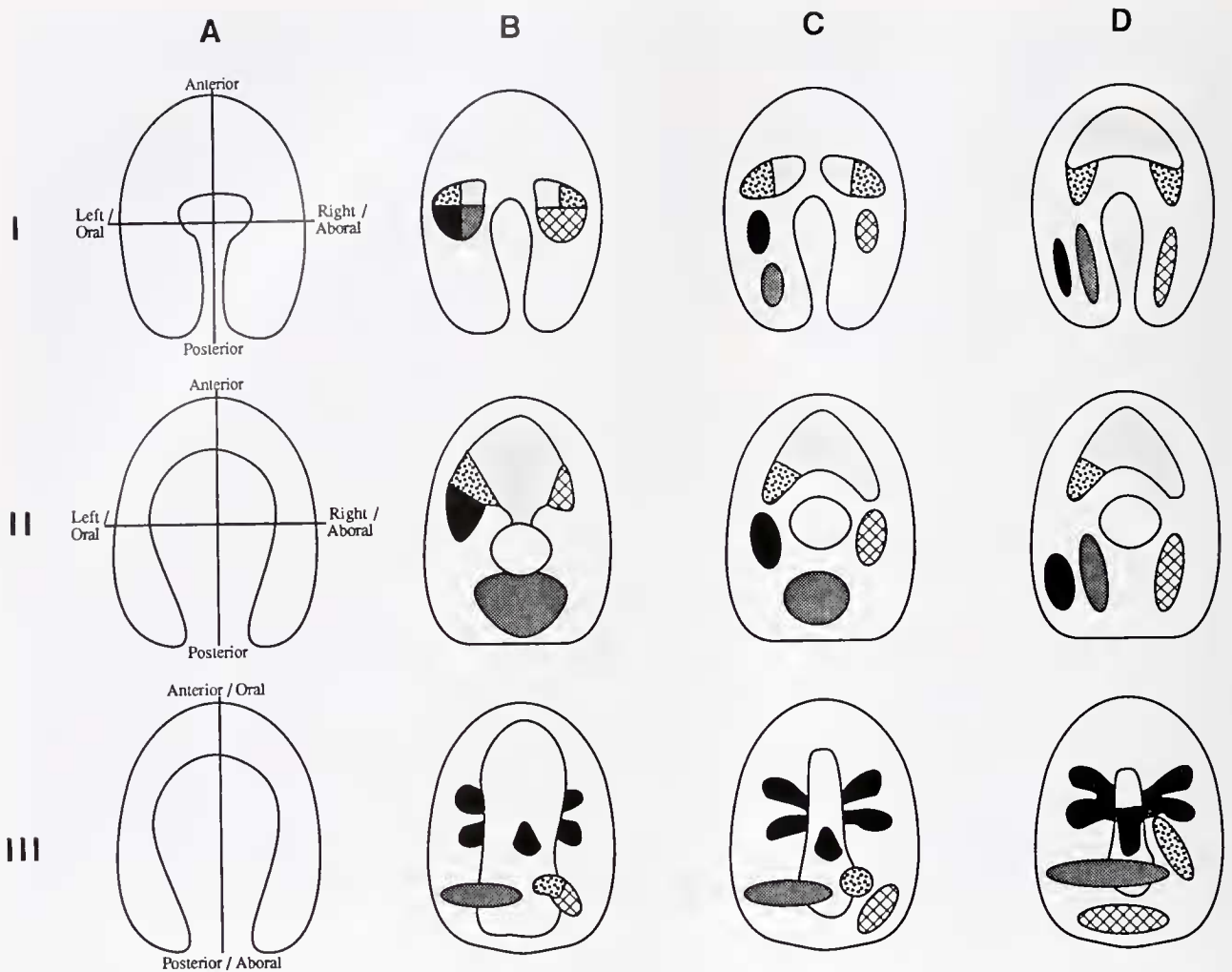


Figure 7. Comparison of coelomic origin and fates during development (A through D) in different asteroids (I, II, and III). All drawings are oriented as dorsal views of longitudinal sections with the anterior end up. A key to the stippling indicating coelomic fates is provided in figure 8. I A–D. Ancestral pattern of coelomogenesis via feeding bipinnarian and feeding brachiolarian larval stages. II A–D. Coelomogenesis in the nonfeeding brachiolarian larvae of the superorder Spinulosacea (e.g. the families Solasteridae and Echinasteridae). III A–D. Coelomogenesis in *Pteraster tessellatus*.

the bipinnaria (e.g., *Astropecten scoparius*, Oguro *et al.*, 1976, p. 561, 566; *Luidia clathrata* Komatsu *et al.*, 1991, p. 497).

Paxillosids with indirect development and pelagic non-feeding larvae. In several asteroid clades, feeding larvae have been replaced by nonfeeding larvae (Strathmann, 1974, 1978). Some species of the order Paxillosida develop from moderately large (about 300–500 μm in diameter) yolky eggs via pelagic nonfeeding larvae. These are termed barrel-shaped larvae because they have a highly simplified external morphology. Barrel-shaped larvae lack brachiolar apparatus and are likely derived from paxillosids with feeding bipinnaria only (Komatsu *et al.*, 1988; McEdward and Janies, 1993). Although few details of internal development are known, coelom formation in barrel-shaped

larvae is similar to the ancestral pattern because it includes the formation of a U-shape and an anterior coelom (Komatsu, 1975, p. 54; 1982, p. 202; Komatsu and Nojima, 1985, p. 276).

Asteroids with indirect development and benthic non-feeding larvae. *Asterina gibbosa* (MacBride, 1896) and *Leptasterias hexactis* (Chia, 1968) develop from large yolky eggs (about 500 μm and 800 μm , respectively) via benthic, simplified, nonfeeding brachiolaria. Coelomogenesis in these species is only slightly modified from the ancestral pattern. A single, large enterocoel evaginates from the anterior tip of the archenteron. This unpaired coelomic sac expands anteriorly and laterally, then extends backwards with a pair (left and right) of short, posterior projections, thus producing the characteristic U-shaped







Pattern	Cavity	Adult fate in the terminology of this paper	Adult fate in the terminology of Hyman, 1955
	Preoral coelom	Resorbed	Resorbed
	Axocoel	Inner oral perihemal coelom Axial perihemal coelom	Inner oral hyponeural sinus Axial sinus
	Hydrocoel	Water-vascular system	Water-vascular system
	Somatocoel	Oral perivisceral coelom Outer oral and radial perihemal coeloms	Hypogastric coelom Outer oral and radial hyponeural sinuses
	Somatocoel	Aboral perivisceral coelom	Epigastric coelom
	Archenteron	Gut	Gut

Figure 8. Key to the stippling patterns used in the coding of internal cavities and their adult fates in figures 3, 4, 6, 7, and 10. This information is cross referenced to the terminology of Hyman (1955).

coelom. The lateral projections eventually give rise to separate coelomic regions (primarily a sagittally oriented hydrocoel on the left side of the larval body and a somatocoel on each side of the larva). The anterior region of the unpaired U-shaped coelomic sac extends into the lumen of the brachiolar arms and is considered homologous to the preoral coelom of feeding larvae (Erber, 1985; Strathmann, 1988).

Asteroids with indirect development and pelagic non-feeding larvae. Several asteroids develop from large eggs (about 1000 μm in diameter) via pelagic nonfeeding brachiolarian larvae (distributed in the orders: Forcipulata, Valvatida, Spinulosida, and Velatida; see Fig. 9) (McEdward and Janies, 1993). There are several studies of internal structure in these larvae (e.g., *Fromia ghardaqana*, Mortensen, 1938; *Crossaster papposus* Gemmill, 1920; *Henricia sanguinolenta*, Masterman, 1902; and *Solaster endeca* Gemmill, 1912). The early pattern of anterior and hydrocoelic coelomogenesis of these brachiolaria is identical to that of the benthic brachiolaria.

Features of coelomogenesis in taxa closely related to Pteraster tessellatus. In an echinasterid, *Henricia sanguinolenta* (Masterman, 1902), and two solasterids, *Solaster endeca* (Gemmill, 1912) and *Crossaster papposus* (Gemmill 1916, 1920), for which there is detailed information on internal features of development, the archenteron constricts into unpaired anterior, middle, and posterior portions (Fig. 7IIA, B). The anterior portion and the posterior portion of the archenteron are presumptive coelom, whereas the middle portion is presumptive gut (Masterman, 1902; Gemmill, 1912, 1920; Hyman, 1955, p. 298). The axocoels, hydrocoels, and right somatocoel develop from the unpaired anterior coelom, as is typical in non-feeding larval development (Fig. 7IIB-D), but the left so-

matocoel develops from the posterior enterocoel (Fig. 7IIB, C) in proximity to its definitive larval location. The anterior, unpaired enterocoel develops from the anterior portion of the archenteron (Fig. 7IIA-IIB). Two long lateral projections extend posteriorly from the anterior enterocoel, producing a U-shaped coelom. In spite of these modifications, many characteristics of the ancestral pattern of asteroid development occur in these species. (1) A hydrocoel pinches off from the left lateral region of the U-shaped coelom. (2) a somatocoel (adult aboral perivis-

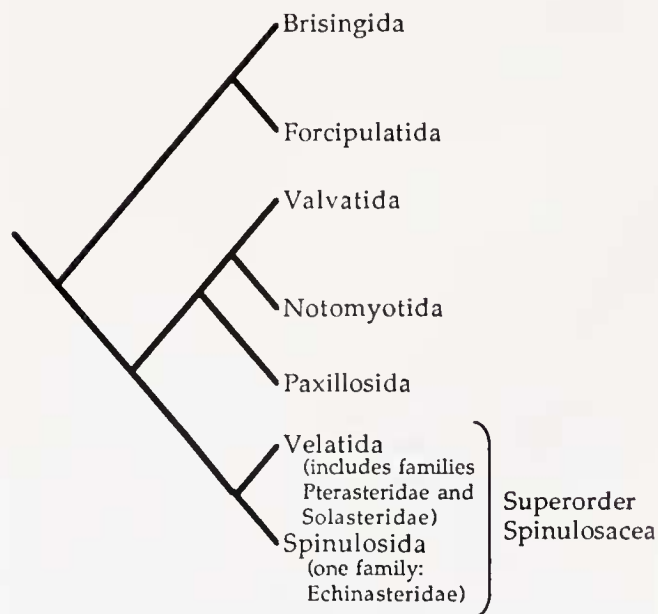


Figure 9. A cladogram of asteroid orders based on Blake (1987). The taxonomic location of the families of the superorder Spinulosacea. This group includes *Pteraster tessellatus* and close relatives.

ceral coelom) forms from the posterior portion of the right side of the U-shaped coelom, (3) the left anterior region of the U-shaped coelom forms the axocoel (adult perihemal coelom of the axial complex and the inner oral perihemal ring coelom), and (4) a preoral coelom lines the brachiolar arms (Fig. 7IIB-D).

One striking difference in the pattern of coelomogenesis in solasterids and echinasterids is a radical departure from the ancestral pattern of coelom development: there has been a change in the site of origin of the left somatocoel. This heterotopic modification, which produces multiple (*i.e.*, anterior and posterior) enterocoels, is a synapomorphy of the asteroids of the superorder Spinulosacea (O. Spinulosida = family Echinasteridae and O. Velatida includes families Solasteridae, Pterasteridae; see Blake, 1987) (Fig. 9).

The evolution of posterior enterocoely dissociated the origin of the left somatocoel from the anterior region of the archenteron, in the lineage leading to *P. tessellatus*. We believe that this modification of coelomogenesis was a necessary precursor to the radical rearrangements of coelomogenesis that occurred in *P. tessellatus* to produce direct development. This was an important preadaptation for the novel positioning and acceleration of water-vascular morphogenesis that occurred in the evolution of pterasterids. Because *P. tessellatus* lacks the bilateral pattern of enterocoely and has instead a radial and transverse pattern, the terms "left" and "right" are inappropriate. Although Gemmill (1912, 1916, 1920) and Masterman (1902) referred to the posterior coelom of the spinulosaceans as the "left posterior coelom" because of homology with the left somatocoel of other asteroid larvae, we refer to this cavity, which is also found in *P. tessellatus*, as the large posterior coelom.

Unity and diversity in asteroid coelomic development. In spite of considerable diversity in external larval morphology, the pattern of coelomic development among asteroids is very conservative, regardless of shifts from feeding to nonfeeding, or from pelagic to benthic development. On the basis of the similarity in anterior coelomic development, Erber (1985) argued that a preoral coelom develops in the anterior region of the larva in all asteroids and that, therefore, a homologous brachiolaria stage occurs throughout the Asterozoa, including species in which brachiolar arms are absent (*e.g.*, paxillosids and *P. tessellatus*). Erber's criterion for brachiolarian development is sufficiently general to include all known asteroids, yet it also leads to at least two conclusions that we believe are false. First, Erber (1985) concluded that paxillosids have a "brachiolarian" stage of development. However, as stated earlier, paxillosids develop as feeding bipinnaria or nonfeeding simplifications thereof—they are not brachiolaria nor are they derived from (*i.e.*, homologous with) brachiolaria (Komatsu *et al.*, 1988). Second, Erber (1985)

assumed that the mode of coelom formation in *P. tessellatus* would be identical to that of its close relatives, the echinasterids and solasterids. This assumption was based, in part, on the prevailing interpretation of the evolution of the "larva" of *P. tessellatus*. Fell (1967, p. S71) considered the absence of brachiolar structures in *P. tessellatus* to be the result of minor simplifications of the external structures of a typical pelagic nonfeeding brachiolarian larva.

In all larval types, most of the anterior of the larva (including the preoral coelomic structures) is resorbed at metamorphosis (Fig. 8). This resorption is accomplished by translocation of the larval structures to the oral side of the juvenile rudiment, followed by histolysis and transfer to the juvenile digestive tract (Chia and Burke, 1978). The postmetamorphic (juvenile and adult) fates of the larval coeloms are highly conservative among asteroids, as illustrated by a comparison of figures 7I and 7II. The left side of the axocoel forms the perihemal coelom of the axial complex and the inner oral perihemal ring coelom (Fig. 7, 8) (Hyman, 1955; Dawydoff, 1948). The left hydrocoel forms the entire coelomic lining of the water-vascular system. The left somatocoel, by growing dorsal and ventral extensions medial to the hydrocoel, forms the oral perivisceral coelom. The outer oral perihemal ring coelom forms from small interradial evaginations of the oral perivisceral coelom. The right axohydrocoel is mostly resorbed at metamorphosis yet becomes the madreporic vesicle (an aboral component of the axial complex) in some species (Hyman, 1955). The right somatocoel lies on the side of the gut opposite the hydrocoel (*i.e.*, on the aboral side of the juvenile) and forms the aboral perivisceral coelom.

Given the conservative nature of asteroid coelomogenesis, analysis of the evolution of direct development can be focused on the transition from the larval pattern of coelomogenesis in the nonfeeding brachiolaria of taxa closely related to *P. tessellatus* (*e.g.*, *Solaster* and *Henricia*) to the highly derived pattern of *P. tessellatus*.

What evolutionary changes in morphogenesis occurred to transform a brachiolarian larva into a mesogen?

Direct development is characterized by the morphogenesis of the juvenile from the embryonic stages and by the complete absence of larval structures in development (McEdward and Janies, 1993). The prevailing view is that evolution of direct development must involve the loss of larval features from the life cycle by the suppression or elimination of larval programs in development (Fell, 1945; Raff, 1987). This hypothesis accurately describes the resultant differences between solasterid or echinasterid brachiolarian larvae and the mesogen of *P. tessellatus*. However, this hypothesis offers little insight into the processes by which the ancestral ontogeny has been modified to

yield the derived ontogeny. One result of eliminating larval features is that juvenile features arise earlier in ontogeny. Direct development cannot evolve simply by accelerating developmental processes. Direct development requires spatial, as well as temporal, changes in morphogenesis because the juvenile must develop from an embryonic rather than a larval organization. We propose that direct development evolved in *P. tessellatus* largely via a series of topological changes in coelomogenesis. These heterotopic changes allowed the embryo (gastrula) to develop into a juvenile coelomic organization, thereby eliminating the larval stage and producing a "recession of metamorphosis" (*sensu* Fell, 1945, see also Raff, 1987).

A hypothesis of coelomic rearrangement. The altered pattern of coelomogenesis underlies all of the important features that characterize direct development in *P. tessellatus*. A relatively simple change in the topology of early coelomic development can account for the loss of bilateral symmetry, loss of the preoral lobe, and the development of the coelomic systems in their adult orientation. The arrangement of hydrocoelic lobes from the archenteron establishes radial symmetry and accounts for the transverse orientation of the juvenile disc and the parallel embryonic and adult axes.

We believe that the radical rearrangement of coeloms in *P. tessellatus* evolved by means of a 90° rotation of the anterior enterocoels from the spinulosacean pattern, relative to the animal-vegetal axis of the archenteron (Fig. 10). This rotation shifted the hydrocoel from its ancestral location on the left side of the body (Fig. 10A) to a central location on the longitudinal (animal-vegetal) axis of the body (Fig. 10B). Consequently, the hydrocoel lobes (radial canal precursors) develop in a transverse plane around the archenteron in *P. tessellatus* (Fig. 10C) rather than in the sagittal orientation typical of all asteroid larvae (Fig. 7I, II).

In conjunction with this hypothesized rotation, the ancestral axocoels fused with the ancestral right somatocoel, and the preoral coelom was lost (Fig. 10B). The site of evagination of the large posterior enterocoel in the spinulosacean pattern was unaffected by the relocation of the anterior enterocoels (Figs. 7, 10).

Our hypothesis has several points in its favor. First, it is consistent with the interpretation of the small posterior enterocoel of *P. tessellatus* as homologous to fused left and right axocoels and right somatocoel of the solasterids and echinasterids (Figs. 7II, III; 10C). The mixed coelomic fates of the small posterior enterocoel in *P. tessellatus* (axial and inner oral perihemal ring coeloms and aboral perivisceral coelom) are the basis for this interpretation (Fig. 8).

Second, the rotation hypothesis is supported by the observation that a 90° rotation to the right (flexion *sensu* Gemmill, 1912) occurs at metamorphosis in all asteroids

with indirect development. Metamorphic flexion shifts the coeloms from the larval arrangement into the juvenile arrangement. We argue that an analogous rotation of the positional information specifying sites of enterocoel formation occurred in the lineage leading to *P. tessellatus*. This effectively shifted the specification of the post-metamorphic coelomic arrangement into the very early stages of development. The result was direct development of the coeloms in the juvenile orientation from the archenteron of the embryo (Figs. 7III; 10). It is not surprising that conservative and fundamental features of asteroid metamorphosis, such as the transformation of coeloms from the larval to the adult organization, should be co-opted into a derived pattern of development in which coeloms arise in their adult orientation.

Third, the rotation hypothesis is attractive in its simplicity; a single alteration of the map for enterocoel formation can explain the derivation of a highly modified pattern of coelomogenesis in the evolution of direct (non-larval) development.

Differences in the site of the origin of enterocoels have occurred in other asteroids. In addition to the solasterids and the echinasterids that were discussed above, there are other documented cases of the heterotopic origin of a posterior coelom: *Patiriella regularis* (Byrne and Barker, 1991, p. 334, 341) and *Marthasterias glacialis* (Gemmill, 1916). Although heterotopy seems to be a rare event, on the basis of the limited developmental diversity that has been documented in asteroids, its occurrence illustrates that the presumptive fates of the regions of the archenteron can be modified evolutionarily.

Our rotation hypothesis leads to a new interpretation of some of the features of *P. tessellatus*. The yolky anterior region of the mesogen has traditionally been interpreted as a preoral lobe (*e.g.*, Chia, 1966; Fell, 1967 p. S71). If rotation of the coeloms occurred as we have suggested, then the anterior region of *P. tessellatus* is not homologous to the preoral lobe of a brachiolarian larva, because it lacks the only defining characteristics of a preoral lobe, namely the preoral extension of the anterior coelom into brachiolar apparatus. We believe that, in *P. tessellatus*, the evolution of fused coelomic regions from opposite sides of the solasterid or echinasterid larva involved the loss of the intervening preoral coelom (Fig. 10B). In our interpretation, the site of origin of the former preoral coelom would correspond to the lateral region of the archenteron, posterior to the hydrocoelic lobes and anterior to the site of formation of the small posterior coelom (this point is denoted by the * on Fig. 10B). The yolky anterior region of the developing *P. tessellatus* is located on the oral surface of the juvenile; it probably functions only as a nutritional store. The extension of the archenteron into the anterior region of the mesogen likely serves as a conduit to deliver nutrients to the gut and is not a preoral coelom.

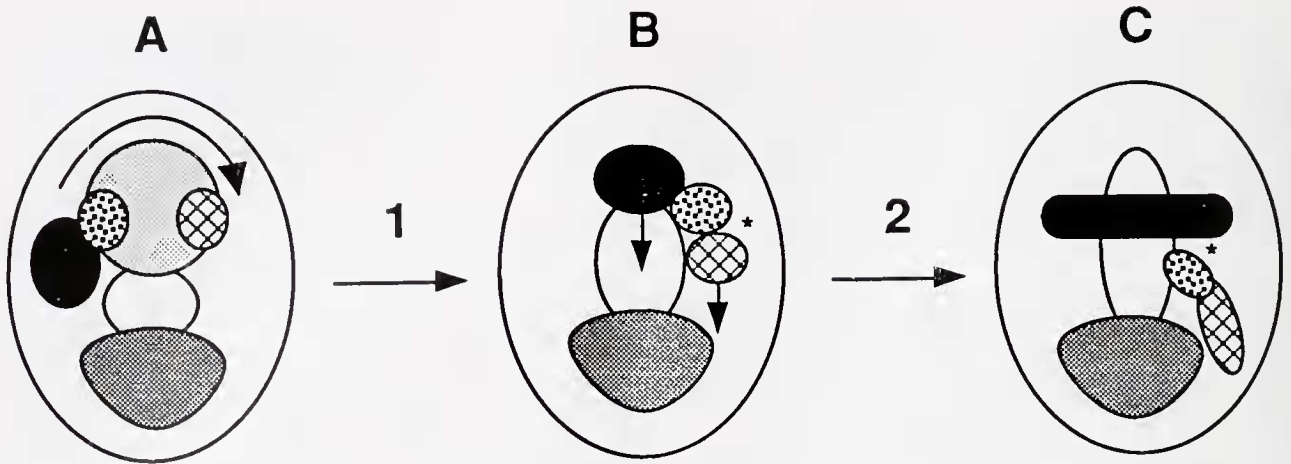


Figure 10. A hypothesized evolutionary sequence of coelomic rearrangements (dorsal view) from the spinulosacean pattern of development (A) to that of *Pteraster tessellatus*. Step 1 involves a simple 90° rotation of the ancestral anterior enterocoels relative to the animal-vegetal axis of the archenteron. This shifted the hydrocoel from its ancestral location on the left side of the spinulosacean embryo (A) to a central location in a hypothesized intermediate form (B). Also in step 1, the ancestral axocoel shifted from an anterior-left-central position (A) to an anterior-right-central position where it fused with the ancestral right somatocoel (B) and became the small posterior enterocoel of *P. tessellatus* (C). This fusion was likely facilitated by the loss of the preoral coelom as noted by the * in stages B and C. Step 2 shows the transition from the hypothesized intermediate form (B) to *P. tessellatus* (C). This could be accomplished by a heterotopic change in the point of origin of the enterocoels from the anterior of the archenteron to the central and posterior locations seen in *P. tessellatus* (C). In this hypothesis the anterior of the archenteron of *P. tessellatus* is a novel feature and not a vestige of a preoral coelom. The posterior site of evagination of the spinulosacean large posterior enterocoel was unaffected by the relocation of the anterior enterocoels.

Comparative morphogenesis in asteroids as a system for studying the evolution of development

P. tessellatus provides an important system for analysis of major evolutionary changes in development, particularly morphogenesis and early pattern formation (e.g., establishment of body axes and symmetry). The alterations in developmental mechanisms associated with the evolution of direct development have recently been approached through a combination of cellular methods (e.g., cell lineage specific gene-expression, cell lineage tracing) and species comparisons (e.g., Jeffrey and Swalla, 1991; Wray and Raff, 1990). Raff (1992) proposed that remodeling of development via changes in the primordial morphogenetic axes of the egg is important in shifts from indirect to direct development. We postulate that just such changes have occurred in the evolution of direct development in *P. tessellatus*. We have documented radical topological changes associated with morphogenesis of juvenile coeloms directly from the embryonic archenteron, rather than from the bilaterally arranged series of larval coeloms. An important component of those changes involved the elimination of larval bilateral symmetry. In solasterid and echinasterid asteroids, larval morphogenesis involves the establishment of a bilateral symmetry that replaces the embryonic radial symmetry. At metamor-

phosis, a new axis of radial symmetry is established for the morphogenesis of the juvenile body. In *P. tessellatus*, the axis of primary embryonic symmetry (radial) is retained as the axis of radial symmetry in the juvenile throughout the development of the mesogen. We postulate that the loss of the larval phase of development and morphogenesis of the juvenile from the embryonic organization may be due, in part, to the elimination of the system for specifying larval left-right and larval dorsal-ventral polarity in the egg and early embryo. Loss of such polarity information would result in a radially symmetrical morphogenetic framework on which to build juvenile coelomic systems and other structures. The relationship between the first cleavage plane and the dorsal-ventral axis is variable among echinoids (Henry *et al.*, 1992), and this has had a mechanistic role in evolutionary changes in development (Henry and Raff, 1990; Henry *et al.*, 1990). These recent findings invite the investigation of changes of morphogenetic axes among asteroids. A comparison of the polarity characteristics of solasterid, echinasterid, and pterasterid eggs and embryos might yield important insights into structural patterning in early development and the mechanisms underlying its evolutionary modification.

Some starfish do not free spawn, but rather brood large yolky nonfeeding young on the benthos. These young de-

velop through larval stages with brachiolarian arms and an adhesive disc, but are not released from the mother until after metamorphosis. Morphological simplification of young might be expected in species with benthic brooding because larvae may be released from selection pressures for effective settlement structures. The morphogenesis of internal structures in brooded asteroids is unknown, so the diversity of developmental modifications that may occur as a result of brooding are not appreciated. An understanding of this diversity is important for assessing whether the evolution of brooding results in specializations and simplifications of morphology and development that are effectively irreversible (as is the case with the loss of feeding larvae, Strathmann, 1978). Alternatively, the evolution of benthic development could eliminate some of the selective pressures on larvae, providing the evolutionary flexibility to generate novel patterns of morphogenesis and thus to allow the re-evolution of pelagic development in new ways despite the loss of larval structures.

Most species of the family Pterasteridae that have been studied hold their eggs under the supradorsal membrane and brood young long into juvenile development. Larval attachment structures were likely lost in the pterasterids after the lineage became very specialized brooders in the deep-sea. Direct development was likely the result of selection for general developmental efficiency, through the elimination of nonfunctional larval features, during a very long history of brooding (see McEdward and Janies, 1993; McEdward, unpubl.). Pelagic development is likely a derived trait in this family.

The comparative study of development among spinulosacean asteroids can directly address the ecological context of evolutionary shifts from indirect to direct development, as well as transitions between pelagic and benthic development. Specifically, comparisons of development among the pelagic brachiolarian larvae from the outgroups Solasteridae and Echinasteridae, the young of a brooding pterasterid, and the pelagic mesogen of *P. tessellatus* would provide a rare opportunity to investigate the role of the evolution of development in the important ecological transition from a nondispersive to a dispersive life history.

Changes in development in conjunction with paedomorphic shifts in the life cycle have potential for the evolution of new body plans. The newly discovered deep-sea concentricycloid echinoderms are characterized by a unique water-vascular geometry of dual circumoral rings (Baker *et al.*, 1986; Rowe *et al.*, 1988). The novel pattern of morphogenesis of the circumoral ring canal in *P. tessellatus*, combined with progenesis, may have provided a mechanism for the evolution of the unique water-vascular geometry of the concentricycloids (Janies and McEdward, in press). We postulate that proximal lateral evaginations

of the radial canal could be duplicated at an early developmental stage to produce dual circumoral ring canals. The duplicated formation of circumoral rings was a likely a key innovation in the evolution of the concentricycloids (Janies and McEdward, in press).

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